LRH: Abdala-Roberts, Moreira, Cervera, and Parra-Tabla

RRH: Light availability and Chemical Defenses in Mahogany

Light Availability Influences Growth-Defense Trade-Offs in Big-Leaf Mahogany (*Swietenia macrophylla* King)

Luis Abdala-Roberts[1]*, Xoaquín Moreira[1,2], José Carlos Cervera[3], and Víctor Parra-Tabla[3]

[1]Department of Ecology and Evolutionary Biology, University of California, Irvine, California, USA 92697

[2]Misión Biológica de Galicia (MBG-CSIC), Apdo. 28, 36080 Pontevedra, Galicia, Spain.

[3]Departamento de Ecología Tropical, Campus de Ciencias Biológicas y Agropecuarias, Universidad Autónoma de Yucatán, Apartado Postal 4-116, Itzimná, 97000 Mérida, Yucatán, México.

*Corresponding author:

Email: labdala@uci.edu

321 Steinhaus Hall, University of California-Irvine

Irvine, CA 92697 USA

Phone: 001 (949) 824-6140

Received_____; revision accepted_____.

ABSTRACT

We report on findings from a common garden experiment showing that the magnitude of change in the production of phenolic compounds in response to different amounts of light availability is tissue-specific in saplings of big-leaf mahogany (*Swietenia macrophylla*). Moreover, we show that trade-offs between growth and the production of chemical defenses emerge only under light-limited conditions. These findings emphasize the need for considering the specificity of plant defensive responses to resource availability, as well as the influence of the abiotic environment (via trade-offs) on plant defense allocation patterns.

Keywords: Allocation constraints; condensed tannins, optimal defense; plant defenses; polyphenolics; resource availability; Yucatan.

Plant responses to biotic and abiotic conditions can be highly specific. For example, the magnitude of induced responses to herbivory may occur only in damaged tissues (Karban 2011), may be tissue-specific depending on the fitness value and the frequency of herbivore attack for each organ and/or tissue (Moreira *et al*. 2012), and may also vary depending on the identity of the herbivore eliciting the damage (Moreira *et al.* 2013). In this sense, the optimal defense theory (ODT) holds that tissues with a higher fitness value (and/or higher risk of herbivory) should be more defended (Zangerl & Bazzaz 1992, Zangerl & Rutledge 1996). However, ODT predictions may be environment-dependent if defensive traits vary in their response to abiotic factors and if such variation is tissue-specific, thus causing shifts in relative allocation of defenses among plant parts. Such context-dependent responses, however, have usually not been addressed in previous studies.

In addition, some studies have found that plant growth and defensive responses can be environment-dependent because of resource allocation constraints (Valladares *et al.* 2007, Sampedro *et al*. 2011). For instance, trade-offs between growth and defense may constrain the ability of plants to respond to environmental changes (reviewed by Herms & Mattson 1992, Simms 1992, Stamp *et al.* 2003), and such trade-offs are typically stronger in resource-poor soils (Cipollini & Bergelson 2001, Koricheva 2002, Donaldson *et al.* 2006, Sampedro *et al.* 2011) or light-limiting environments (Osier & Lindroth 2006; Rodríguez-García & Bravo 2013). The rationale for this is that defenses are costly to produce, and it is thus expected that resource allocation constraints between growth and defense should become stronger or more evident under resource-limited conditions (Herms & Mattson 1992).

Big-leaf mahogany (*Swietenia macrophylla* King, Meliaceae) is a self-compatible neotropical tree that is monoecious and produces unisexual flowers (Styles & Khosla 1976;

Pennington & Sarhukán 2005). Fruits are woody capsules containing wind-dispersed seeds (Pennington *et al.* 1981). It exhibits high outcrossing rates and relatively low population genetic differentiation (Loveless & Gullison 2003). Previous work has shown that recruitment takes place primarily in natural (*e.g.* forest gaps) or human-induced open sites (Lamb 1966, Gullison *et al.* 1996, Snook 1996), suggesting that this species is light-demanding during early life stages (Medina *et al.* 2003). In this study, we assessed changes in growth and chemical defenses across different types of tissue (leaves and stems) in big-leaf mahogany saplings from seven source populations grown under contrasting light regimes. We chose light availability because this factor is an important modulator of investment in defenses by plants, particularly phenolic compounds (reviewed by Ballaré *et al*. 2012, Ballaré 2014), and because such responses are expected to be important in light-demanding species such as mahogany. First, we examined the specificity of defensive responses to light availability by comparing the total production of polyphenolic compounds and condensed tannins in leaves and stems from saplings grown under different light environments. Second, we evaluated the presence of growth-defense trade-offs as well as if such trade-offs were influenced by light availability. Because the production of defenses is expected to be costly, we predicted that trade-offs would arise only under conditions of low light availability. We chose total polyphenolics and condensed tannins as measures of defenses because their production is strongly influenced by light availability (Ballaré *et al*. 2014), and because they represent a major group of chemical compounds acting against herbivores feeding on *S. macrophylla* (Pérez-Flores *et al*. 2012), as well as other species of Meliaceae (Arnason *et al*. 2004).

In late March 2012, we collected seeds from seven trees located in southern Quintana Roo (SE México; see Table S1). Distance among trees spanned from 3 to 50 km

which parallels the distance used by previous studies to define genetically distinct populations of this species (*i.e.* ≥ 3 km; Gillies *et al.* 1999, Loveless & Gullison 2003). Thus, this sample of trees was representative of inter-population variation at a regional scale. Hereafter we refer to all offspring from a maternal tree as a population source. In late June 2012, we germinated 40 seeds per mother tree in 1-l bags filled with a mix of native soil and peat moss (1:1), and kept them for two months in a greenhouse at the Universidad Autónoma de Yucatán (20°52′3″ N, 89°37′26″ W; Campus de Ciencias Biológicas y Agropecuarias [CCBA], SE Mexico). In early September 2012, we transferred 20 seedlings per population source ($N = 140$) to 15-l bags filled with native soil and placed them outside of the greenhouse under partially shaded conditions to achieve acclimation to increased light availability. In early October 2012, we moved bagged seedlings to an experimental site located at the CCBA which was surrounded by a matrix of secondary tropical forest.

The experiment consisted of a split-plot design composed of three 3 × 5-m^2 plots separated by a distance of 1.5 m, oriented from east to west. Each plot was further divided into two 1.5 × 2.5-m^2 subplots. Distance among plants within each subplot was 0.5 m. Southern subplots were covered with a nylon mesh placed 2.5 m above the ground and on the sides (hereafter "shaded" treatment). Northern subplots were not covered and experienced natural light levels (hereafter "ambient light" treatment). Although this approach would potentially confound subplot position with treatment level, we intentionally assigned subplots of the each treatment to the same (north or south) position because the surrounding vegetation on the south side of the plots was higher than on the north side and partially shaded those subplots. If subplots had been randomly or systematically assigned to each light treatment then some subplots of the non-shaded

1 treatment would have been on the south side and thus under partially shaded natural
2 conditions, thus making our light treatment largely ineffective.
3 The mean percent of photosynthetic photon flux density (PPFD) reaching plants in
4 ambient light and the shaded environment was 75.2 ± 1.1% (mean ± S.E.) and 41.4 ± 0.7%,
5 respectively of the total available PPFD at full sunlight (45.4 mol m^2/d). Means are based
6 upon measurements for each plot and treatment level recorded every 10 min from dawn to
7 dusk during five consecutive days. PPFD was measured with quantum sensors (LI-190SB,
8 LI-COR, Lincoln, Nebraska, USA) connected to a data logger (CR21X, Campbell
9 Scientific, Logan, UT, USA). Treatments mimicked two levels of light availability
10 experienced by big-leaf mahogany saplings in tropical dry forests: a forest gap (ambient
11 light) and a partially shaded forest understory (shaded). Seedlings of each population
12 source (10 plants per source, per light treatment) were randomly allocated among plots,
13 subplots, and treatment levels.
14 To minimize unintended effects of artificial shading on water availability, we
15 maintained soil humidity constant by watering plants four to five times per week. We found
16 that on average, transpiration rates were higher for plants in the ambient light treatment at 9
17 AM and midday (3.4 ± 0.2 and 1.7 ± 0.3 μmol/m^2/s, respectively, data are mean ± SE) than
18 for the shaded treatment (2.4 ± 0.2 and 1.4 ± 0.2 μmol/m^2/s). Similarly, photosynthetic
19 rates were also higher for the ambient light treatment (1.9 ± 0.2 and 5.3 ± 0.5, μmol/m^2/s)
20 than for the shaded treatment (0.4 ± 0.2 and 3.1 ± 0.4, μmol/m^2/s). These data show that
21 plants under ambient light had greater stomatal opening, which is not expected for a water-
22 stressed plant. For these plants, a greater stomatal opening led to a higher carbon gain.
23 Therefore, photosynthetic rates were light-limited and not water-limited under both

treatments and suggest that any effects of light availability on growth and defenses would not be due to differences in water availability.

We measured the number of new leaves produced per plant in late October 2012 (initial measurement), mid November 2012, and early January 2013. Subsequently, towards the end of the experiment in mid June 2013, we measured plant height. Although herbivore presence was not experimentally controlled, only 17 plants exhibited some evidence of herbivore damage (in leaves or stem) throughout the sampling period. Excluding these plants from the analysis of final height and leaf production did not change the results; therefore we included them in the statistical analyses. In early July 2013, we collected two fully expanded young leaves and a 5-cm long portion of the stem of 10-12 plants (with no evidence of herbivory) per population source (half in each light treatment level) to quantify the concentration of total polyphenolics and condensed tannins in each plant tissue. Both polyphenolics and condensed tannins are widely recognized as herbivore feeding deterrents across many plant taxa (Marquis 1992, Salminen & Karonen 2011, Mithöfer & Boland 2012, Moreira *et al*. 2014), and have been shown to negatively affect growth and reproduction of insect herbivores that feed on big-leaf mahogany (*e.g. Hypsipyla grandella*, Lepidoptera; Pérez-Flores *et al.* 2012). Accordingly, they are likely an important defensive trait in mahogany seedlings where insect and vertebrate herbivory have a large impact on seedling survival (Grogan *et al.* 2003, Norghauer *et al.* 2010).

Total polyphenolics were extracted and analyzed as described by Moreira *et al.* (2012). Briefly, total polyphenolics were extracted from 300 mg of plant tissue with aqueous methanol (1:1 vol:vol) in an ultrasonic bath for 15 min, followed by centrifugation and subsequent dilution of the methanolic extract. Total phenolic concentration was determined colorimetrically by the Folin-Ciocalteu method in a Biorad 650 microplate

reader (Bio-Rad Laboratories Inc., Philadelphia, PA) at 740 nm, using tannic acid as standard, and concentrations were based on dry weights. Condensed tannins were quantified by the acid butanol method (Porter *et al*. 1986) in the same 50% aqueous methanol extract used for polyphenolics. A mixture of an aliquot of methanol extract and acid butanol (950 ml of n-butanol mixed with 50 ml of concentrated HCl) and iron (0.5 g of 2% ferric ammonium sulphate in 2N HCl) reagents was placed in a boiling water bath for 50 min and then cooled rapidly to 0ºC on ice. Condensed tannins were determined colorimetrically in a Biorad 650 microplate reader at 550 nm using a commercial quebracho tannin extract (72.0% condensed tannins) as standard (Sampedro *et al*. 2011).

The effects of plot (fixed), light treatment (fixed), population source (random), population source × light (random), and plot × light (random) on final plant height, total leaves produced, concentration of total polyphenolics, and concentration of condensed tannins were analyzed with a mixed model solving for split-plot designs according to Littell *et al.* (2006) using PROC MIXED in SAS ver. 9.2 (SAS Institute Cary, NC). Variance components of random effects were estimated with restricted maximum likelihood as this method is appropriate for calculating appropriate standard errors for model estimators and least square means in unbalanced designs (Littell *et al*. 2006). The statistical significance of each random effect was assessed using likelihood ratio tests, where the difference in -2 times the log-likelihood of models including and excluding each random effect is distributed as one tailed χ^2 test with one degree of freedom (Littell *et al.* 2006). The models for total polyphenolics and condensed tannins also included the effect of tissue (leaf or stem, fixed), tissue × treatment (fixed), and plant (random) nested in population source; including the plant effect accounted for the non-independence of tissue samples drawn from the same plant. If the tissue × treatment interaction was significant, we performed two sets

of component models: a) one comparing defenses between tissues separately within each light treatment level to test for a difference in relative allocation to defenses between leaves and stems under shade vs. ambient light conditions, and b) another comparing defenses across light treatments separately within each tissue to assess if there were differences in the magnitude of the response to light availability between leaves and stems.

We explored growth-defense trade-offs separately under ambient light and shaded conditions using population least-square means (from the above models) and regressing concentration of total polyphenolics or condensed tannins (using means across tissues) onto leaf production and plant height. We used the mean concentration of polyphenolics or condensed tannins across types of tissue (as opposed to running separate regressions for stems and leaves) because this provided an overall measure of defensive status at the plant level. Averaging values across tissues yielded qualitatively similar results compared to analyses performed separately for leaves and stems, i.e. averaging values across tissues did not mask tissue-specific patterns. The latter is further supported by a positive relationship for concentration of chemical defenses between leaves and stems (total polyphenolics: $R^2 = 0.60$, $P = 0.001$; condensed tannins: $R^2 = 0.40$, $P = 0.01$). All general linear models and regressions were based upon a normal distribution (normality was evaluated in each case by visual inspection of residuals and Shapiro-Wilk tests). We report model least-square means and S.E. from general linear models as descriptive statistics.

We found marginally significant effects of the light treatment on plant height and leaf production (Table 1). The former exhibited a 16% greater mean value (ambient light: 119.49 ± 3.00 cm; shaded: 103.47 ± 3.02 cm) under ambient light relative to shaded conditions, whereas the mean number of new leaves produced was nearly two-fold (97%) greater under ambient light (ambient light: 13.27 ± 1.00 leaves; shaded: 6.72 ± 0.98 leaves).

We also observed a significant effect of population source on the production of new leaves, but not on plant height (Table 1); the former varied up to two-fold (100%) among populations (5.86 ± 1.87 to 12.32 ± 1.81). We did not find differences in the magnitude of the response to light availability among population sources for either plant height or leaf number (i.e. non-significant population × light interaction; Table 1).

The concentration of total polyphenolics was 88% greater under ambient light (73.65 ± 4.65 mg/g) relative to the shaded environment (39.19 ± 4.62 mg/g) (i.e. significant treatment effect; Table 1). We found significant differences between types of tissue (Table 1), with leaves exhibiting a 63% greater mean value (69.26 ± 2.97 mg/g) than stems (42.40 ± 2.93 mg/g). Moreover, the magnitude of change in the concentration of polyphenolics differed between tissues (i.e. significant tissue × light treatment interaction) (Table 1), with leaves showing a greater difference in the concentration of polyphenolics (94 percent) under ambient light relative to shaded conditions compared with stems (53 percent difference among light treatments) (Fig. 1A). Component analyses within each tissue showed that the concentration of polyphenolics in leaves was significantly greater under ambient light relative to shaded conditions (leaves: $F_{1,2} = 54.77$, $P = 0.01$), whereas for stems the difference between light treatments was not significant ($F_{1,2} = 5.17$, $P = 0.15$) (Fig. 1A). Component analyses within each light environment showed that the concentration of polyphenolics was higher in leaves than in stems under both light treatments (ambient light: $F_{1,39} = 40.12$, $P < 0.0001$; shaded: $F_{1,39} = 10.80$, $P = 0.002$), although the magnitude of difference was greater under ambient light (1.74-fold) than in shaded conditions (1.42-fold) (Fig. 1A). We found no effect of population source or population variation in the response to light availability for the concentration of polyphenolics (Table 1).

Results for condensed tannins were similar to those previously described for total polyphenolics, with ambient light having a 62% higher mean value (56.69 ± 3.85 mg/g) relative to the shaded environment (34.91 ± 3.93 mg/g) (i.e. significant treatment effect; Table 1), and leaves (51.25 ± 3.62 mg/g) exhibiting a 27% higher mean value than stems (40.35 ± 23.66 mg/g) (significant tissue effect; Table 1). Similarly, we found a marginally significant tissue × light interaction (Table 1), following the same pattern as for total polyphenolics with leaves showing a greater (88%) difference in mean values between light treatments (ambient light: 66.21 ± 4.93 mg/g; shaded: 36.28 ± 4.99 mg/g) relative to stems (40% difference between treatments: ambient light: 47.17 ± 4.94 mg/g; shaded: 33.53 ± 5.10 mg/g) (Fig. 1C). As a result, the concentration of condensed tannins was very similar between tissues under shaded conditions (only 8% greater for leaves), whereas in the ambient light treatment leaves exhibited a 40% greater mean value relative to stems (Fig. 1C). Finally, we found no effect of population source or population variation in the magnitude of response to light availability for condensed tannins (Table 1).

Importantly, we found a significant negative relationship between the production of new leaves and the concentration of polyphenolics in shaded conditions (polyphenolics = –1.66*leaf number + 51.49; $R^2 = 0.63$, $P = 0.03$), but not under ambient light ($R^2 = 0.05$, $P = 0.64$) (Fig. 1B), suggesting that light availability influences growth-defense trade-offs in mahogany. We did not find evidence of a trade-off between production of polyphenolics and final height, and this result was consistent across both light treatments (ambient light: $R^2 = 0.03$, $P = 0.73$; shaded: $R^2 = 0.04$, $P = 0.66$). Similarly, we found a tendency for a negative relationship between the concentration of condensed tannins and leaf production under shaded conditions ($R^2 = 0.44$, $P = 0.10$) but not under ambient light ($R^2 = 0.001$, $P =$

0.98) (Fig. 1D). We found no relationship between condensed tannins and final height in either light environment (ambient light: $R^2 = 0.05$, $P = 0.62$; shaded: $R^2 = 0.11$, $P = 0.45$).

Our results indicate that growth of big-leaf mahogany saplings was reduced under shaded conditions compared to ambient light. Accordingly, earlier work by Lamb (1966), Gullison *et al.* (1996), and Snook (1996) suggested that although this species is partially shade-tolerant (see also Grogan *et al.* 2003, Medina *et al*. 2003), seedlings are light-demanding and performance is highest in open sites, such as forest gaps. On the other hand, while leaf production varied significantly among populations, plant height and chemical defenses did not which suggests low genetic variation and differentiation among the sampled populations, as reported previously for this species (Loveless & Gullison 2003). Reduced genetic variation among populations may in turn constrain the potential for genetic variation in growth-related and defensive responses for this species, at least during early life stages, and this may be given by the lack of population variation in the magnitude of the response for the measured trait (n.s. population source × treatment interaction). Nonetheless, further studies with increased population replication across a broader geographical range and including multiple age classes are warranted in order to rigorously test this affirmation.

The higher concentration of total polyphenolics and condensed tannins observed under high light availability is a common response reported in previous studies (reviewed by Ballaré et al. 2014), and has been attributed to the role of phenolic compounds in photo-protection (Mole & Waterman 1988, Karageorgou & Manetas 2006). However, our study provides one of the few examples of plant tissue-specific responses to light availability in terms of concentration of phenolics. Specifically, mahogany leaves - but not stems - produced a significantly higher concentration of total polyphenolics under high light

availability. Moreover, the magnitude of difference in defenses between tissues was almost twice as large under ambient light relative to shaded conditions. A similar pattern was observed for concentration of condensed tannins. The implications of these findings are two-fold. First, that the degree of canalization of phenolic compounds is tissue-specific (*i.e*. less plastic in stems). Based on this, we would predict contrasting effects of light availability on different insect herbivore guilds feeding on big-leaf mahogany. For example, specialist lepidopteran leaf miners (*Phyllocnistis meliacella*, Gracillaridae; Becker 1976) and leaf chewers (*Steniscadia poliophaea*, Noctuidae; Norghauer *et al*. 2010) should be more strongly influenced than specialist stem borers (*H. grandella*, Pyralidae; Newton *et al*. 1993). Second, that patterns of allocation to phenolic compounds are contingent upon magnitude of change in such traits under different abiotic conditions. In our case, tissue-specific differences in the magnitude of change in concentration of phenolic compounds results in smaller differences in relative allocation to these compounds between plant parts under light-limited conditions. Such findings call for future tests of plant defense theory (*e.g.* ODT) that explicitly test for the influence of the abiotic context on within-plant defense allocation patterns.

Findings from this study also suggest context-dependent trade-offs between growth and the production of polyphenolics and condensed tannins in saplings of big-leaf mahogany. Since Julia Koricheva's influential meta-analysis more than a decade ago (Koricheva 2002), it has become clear that tests of trade-offs must necessarily account for environmental effects, as plant allocation constraints may vary depending on resource availability. Over the last few years, evidence has mounted for the effect of soil resources in shaping plant growth-defense trade-offs (*e.g.* Donaldson *et al.* 2006, Sampedro *et al.* 2011). Fewer studies, however, have evaluated the role of light availability in shaping these

allocation constraints (but see Osier & Lindroth 2006). Our findings support the view that phenolic compounds are costly to produce and that such constraints are present in big-leaf mahogany but arise only under light-limited environments. Based on this, we suggest that light availability will set limits to growth and/or production of defenses in this species. Moreover, as explained above, it is important to consider that the underlying mechanism for the observed trade-off could be photo-protection conferred by phenolic compounds and have nothing to do directly with plant defenses against herbivores. Accordingly, plant phenotypic adjustment to increased light availability would result in greater production of phenolic compounds which would in turn influence herbivory (*e.g.* Close *et al*. 2003).

Finally, it is important to consider that our measure of defenses was based exclusively on total polyphenolics and condensed tannins. However, it is possible that light availability has differential effects on other specific groups of phenolic compounds that were not measured (*e.g.* lignins, flavonoids), as well as other classes of compounds (*e.g.* alkaloids, terpenes), some of which (e.g. triterpenes) have been shown to act as strong feeding deterrents of insect herbivores in Meliaceae (Arnason *et al*. 2004). Accordingly, future work is needed to provide a more detailed and precise evaluation of changes in the defense profile of big-leaf mahogany in response to differences in light availability.

Overall, our findings show that predictions by defense allocation theory such as ODT may be contingent upon environmental conditions if the production of defenses is responsive to abiotic factors, as well as tissue-specific. In addition, our work is among the few to show that light availability might drive plant resource allocation trade-offs and thus relative investment in plant functions such as growth and defenses. These findings are relevant for understanding how abiotic forces shape mahogany-herbivore interactions by shaping not only the defensive phenotype as well as the ability of plants to tolerate damage

(because growth responses may be constrained by investment in defenses). Moreover, for light demanding tree species such as mahogany, seedling establishment is a key process that determines lifetime fitness, not only because of herbivore pressure (major cause of juvenile mortality), but also due to intense competition for light in the understory of forest gaps. Therefore, opportunity costs in light-demanding species are expected to be high and strongly determined by the light environment.

ACKNOWLEDGMENTS

The authors would like to thank N. Salinas for assistance in the field and laboratory, R. Mena, V. Solís, L. Esquivel, and D. Marrufo for laboratory assistance, and L. Pato for help with chemical analyses. Dr. Rafael Zas facilitated laboratory equipment and material for the chemical analyses at the Biological Mission of Galicia-CSIC (Spain). We also thank two anonymous reviewers who commented on a previous version of the manuscript. This research was supported by a CONACyT grant awarded to VPT (128856). LAR was funded by a GAANN fellowship and a UCMEXUS-CONACyT scholarship. XM received financial support from Postdoctoral Fulbright/Spanish Ministry of Education grant program.

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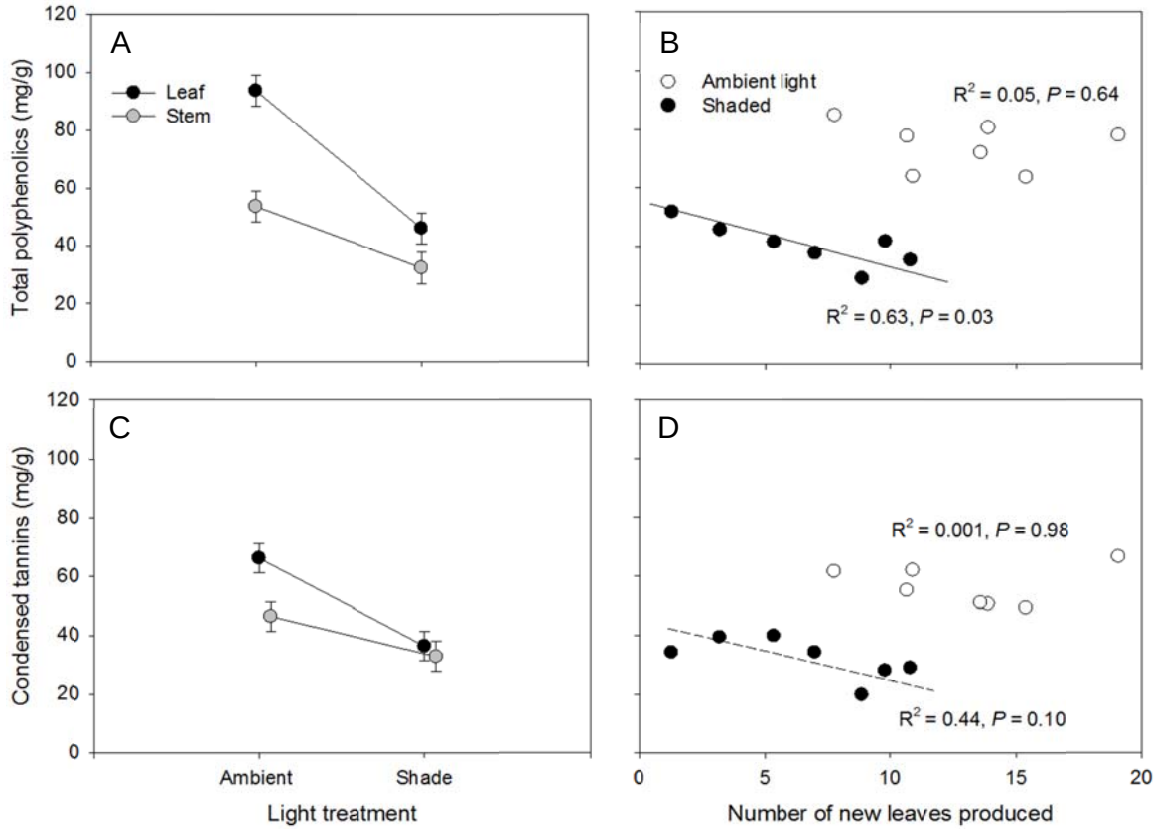
*Table 1. Effects of light availability, population source, and their interaction on growth (final height, leaf production), and defenses (total polyphenolics, condensed tannins) of big-leaf mahogany (*Swietenia macrophylla*) saplings. The model for polyphenolics and condensed tannins also tested for the effects of plant tissue (leaf or stem) and tissue × light treatment. The significance of random effects (population, population × light treatment) was assessed with log-likelihood ratio tests (Littell* et al. *1996). All models included the plot × light treatment interaction as a random effect (results not presented) to test for light treatment based on the appropriate F-ratio and degrees of freedom for fixed effects for a split-plot design. Significant effects (*$P \leq 0.05$*) are in bold, while marginal effects (*$0.05 < P < 0.10$*) are in italics.* F*-values (for fixed effects) or* χ^2 *values* (*for random effects, denoted with a "†") are shown, as well as* P*-values (in parenthesis). NT = effect not tested.*

	Response variable			
Predictor	Final height	Leaf production	Total polyphenolics	Condensed tannins
Light	14.13 *(0.06)*	10.34 *(0.08)*	29.09 **(0.03)**	17.49 (**0.05**)
Population source†	0 (--)	3.6 **(0.05)**	0 (--)	0.3 (0.58)
Source × light†	0.90 (0.34)	0.10 (0.75)	0 (--)	0 (--)
Tissue	NT	NT	45.88 **(< 0.001)**	6.08 (**0.01**)
Tissue × light	NT	NT	11.02 **(0.001)**	3.40 (*0.06*)

FIGURE LEGENDS

FIGURE 1. Left side panels (A, C) show the effect of light availability on the amount of total polyphenolics (mg/g) (A) and condensed tannins (mg/g) (C) in leaves and stems of big-leaf mahogany (*Swietenia macrophylla*) saplings. We found a significant tissue × light treatment interaction for which a difference in the concentration of polyphenolics between light treatments was observed for leaves but not stems, and where the difference in the concentration of polyphenolics between tissues was significant only under the ambient light treatment. For condensed tannins we observed a similar pattern, although the tissue × light treatment interaction was marginally significant. Dots are general linear model least-square means and standard errors. Right side panels show the relationship between the production of new leaves (proxy of plant growth) and the concentration of total polyphenolics (mg/g; average across leaves and stems) (B), and between the production of new leaves and condensed tannins (mg/g; average across leaves and stems) (D) for big-leaf mahogany. A trade-off between leaf production and chemical defenses was observed only under shaded conditions. The relationship between condensed tannins and leaf production under shaded conditions showed a tendency for a negative relationship ($P = 0.10$), and this is indicated by a dashed line representing the relationship predicted by the regression model. Dots are population source least-square means from the general linear models.

Figure 1.


A
Leaf
Stem
Total polyphenolics (mg/g)
120
100
80
60
40
20
0
B
Ambient light
Shaded
R^2 = 0.05, P = 0.64
R^2 = 0.63, P = 0.03
C
Condensed tannins (mg/g)
Ambient
Shade
Light treatment
D
R^2 = 0.001, P = 0.98
R^2 = 0.44, P = 0.10
0
5
10
15
20
Number of new leaves produced